Generic Placement of Species Excluded from *Arabidopsis* (Brassicaceae)

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ABSTRACT. All 59 binomials previously assigned to *Arabidopsis* are critically evaluated and placed in 14 genera, of which *Crucihimalaya*, *Olimarabidopsis*, and *Pseudoarabidopsis* are described as new. Nine new combinations in *Crucihimalaya*, three in *Olimarabidopsis*, and one in *Pseudoarabidopsis*, as well as 12 new synonyms, are proposed. A key to all genera most commonly confused with *Arabidopsis*, including the three new proposed herein, is presented.

Generic delimitation in the Brassicaceae (Cruciferae) is one of the most difficult and often controversial aspects in the systematics of the family (Al-Shehbaz, 1973, 1984; Rollins, 1993; Schulz, 1936). Perhaps the two principal reasons for this are: (1) Convergence in basically every morphological character is so high that superficially very similar genera might well turn out to be remotely related or unrelated upon critical examination of so-called key generic characters and independent assessment of phylogenetic relationship using molecular comparisons (as in the genera herein segregated from *Arabidopsis*). (2) Although the family exhibits tremendous diversity in fruit morphology, other parts of the plant, especially the flowers, usually do not show much diversity and, therefore, there are few morphological characters that can be used to determine relationships. Characters of flowers and vegetative parts have often been ignored or overlooked. Because fruit morphology has traditionally been used in taxonomic treatments of the Brassicaceae, the problem becomes more acute among the numerous genera with relatively similar linear-shaped fruits. In cases like these, vegetative or floral characters could easily be of greater significance than fruit or seed characters in delimiting natural genera.

Given the great interest in *Arabidopsis thaliana* (L.) Heynhold as a model experimental organism, it is of particular value to define clear phylogenetic groupings among its related genera. The limits of *Arabidopsis* (DC.) Heynhold have been the subject of continuous controversy, and many authors (e.g., Al-Shehbaz, 1988; Hedge (in Hedge & Rechinger), 1968; Price et al., 1994) called for the need to establish well-defined boundaries between the genus and its relatives. Although O'Kane and Al-Shehbaz (1997) retained only nine species in *Arabidopsis*, the generic placement of 50 of the 59 binomials previously assigned to *Arabidopsis* remained to be established. The present paper addresses this problem, and keys for the determination of taxa most often confused with *Arabidopsis* are provided.

Molecular comparisons of both chloroplast DNA (Price et al., 1994, unpublished) and nuclear Internal Transcribed Spacer (ITS) regions (O'Kane et al., 1995, 1997, unpublished) have consistently supported dividing the core group of the broadly circumscribed *Arabidopsis* (e.g., table 1 of Price et al., 1994) into a small number of well-separated clades, most notably *Arabidopsis* sensu stricto (including *Hylandra* A. Löve and *Cardaminopsis* (C. A. Meyer) Hayek; see O'Kane & Al-Shehbaz, 1997; Mummenhoff & Hurka, 1995), *A. pumila* (Stephan) N. Busch and relatives (here newly described as *Olimarabidopsis*), and *A. himalaica* (Edgeworth) O. E. Schulz and relatives (here newly described as *Crucihimalaya*). All of these genera belong to a major terminal clade, including a number of other Eurasian and American genera such as *Capsella* Medikus, *Neslia* Desvaux, *Erysimum* L., *Malcolmia* R. Brown, and *Halimolobos* Tausch. Several other species sometimes placed in *Arabidopsis* have been found to belong to the distantly related genera *Thel-*

lungiella O. E. Schulz (Al-Shehbaz & O'Kane, 1995; Galloway et al., 1998) and *Neotorularia* Hedge & J. Léonard (Al-Shehbaz & O'Kane, 1997), or in one case to the genus *Erysimum* (Al-Shehbaz, 1994), which is closely related to *Olimarabidopsis*. Although the taxonomy of *Arabidopsis* has now been worked out at the generic level (O'Kane & Al-Shehbaz, 1997), our research indicates that *Arabis* is polyphyletic and consists of at least three unrelated clades.

Following up the suggestions of new phylogenetic groupings provided by molecular comparisons, we have thoroughly reexamined the morphology of the species previously placed in *Arabidopsis* in order to reassess morphological groupings of species and to try to find morphological characters distinguishing the groups indicated by molecular comparisons. Over the last seven years, we have critically examined more than 6000 specimens from numerous herbaria. We have found that differences in fruit morphology (terete vs. flattened) and seed morphology (incumbent vs. accumbent cotyledons and winged vs. unwinged seeds), which have been previously used (e.g., Busch, 1909; Ball, 1993; Jones, 1964; Mulligan, 1995; Rollins, 1993; Schulz, 1936) to separate the traditionally circumscribed genera *Arabidopsis* and *Arabis*, appear to be very unreliable in the delimitation of natural generic groups. Seven of the nine species of *Arabidopsis* sensu stricto have flattened fruits and accumbent cotyledons, while two have terete fruits and incumbent cotyledons (O'Kane & Al-Shehbaz, 1997). In contrast, differences in trichome branching, flower color, and nature of the cauline leaf base appear to be much more useful in defining natural generic groups among species previously placed in *Arabidopsis* sensu lato. Combinations of these characters, along with molecular phylogenetic data, support the retention of 9 species in *Arabidopsis* and the segregation of 13 species commonly placed in the genus into three new, well-defined genera herein proposed as *Crucihimalaya*, *Olimarabidopsis*, and *Pseudoarabidopsis*. Based on chloroplast DNA sequencing (Price, unpublished), *Olimarabidopsis* is most closely related to *Erysimum*, and both are readily separated from *Arabidopsis* by having yellow or orange (rarely cream or purplish) flowers and malpighiaceous and/or sessile stellate trichomes (*Erysimum*) or submalpighiaceous and subsessile stellate trichomes (*Olimarabidopsis*).

Only 3 of the 14 genera to which the 59 *Arabidopsis* binomials belong are not included in the following key. These, *Murbeckiella* Rothmaler, *Sisymbriopsis* Botschantsev & Tzvelev, and *Robeschia* Hochstetter, are unrelated to *Arabidopsis*. *Murbeckiella* has auriculate cauline leaves, keeled valves, veined septa, and winged seeds, whereas *Arabidopsis* has petiolate cauline leaves, rounded or flat valves, veinless septa, and wingless seeds. *Sisymbriopsis* has pubescent, quadrangular fruits and prominently 3-veined valves, whereas *Arabidopsis* has glabrous, terete or flattened fruits and veinless or obscurely 1-veined valves. Finally, *Robeschia* has dendritic trichomes, 2-pinnatisect or 2-pinnate leaves, much thickened fruiting pedicels as thick as the fruit, and an obsolete style, whereas *Arabidopsis* has simple and stalked forked trichomes, undivided to pinnatifid leaves, slender fruiting pedicels narrower than the fruit, and distinct styles. These three genera have not yet been subjected to molecular studies, but should be analyzed in the near future.

The circumscriptions of *Arabis* and *Halimolobos* in the following key follow that of Rollins (1993). We are, however, aware that these genera, as presently delimited, represent very heterogeneous assemblages of species groups that will have to be re-assigned to other genera, most of which have already been proposed. We are currently working on these groups.

ARTIFICIAL KEY TO THE GENERA WITH MEMBERS FORMERLY PLACED IN *ARABIDOPSIS* SENSU LATO

1a. Plants completely glabrous; leaves and stems glaucous; plants often restricted to strongly saline and/or calcareous soil . . . . . *Thellungiella*
1b. Plants sparsely to densely hairy; leaves and stems not glaucous; plants usually on other soil types.
  2a. Trichomes sessile and completely appressed, malpighiaceous and/or stellate with unbranched rigid straight rays . . . . . *Erysimum*
  2b. Trichomes short- or long-stalked, simple or branched, if stellate and sessile then rays slender and/or branched.
    3a. Scapose annuals without cauline leaves; fruiting pedicel nearly as thick as fruit . . . . . *Drabopsis*
    3b. Nonscapose annuals, biennials, or perennials with few to many cauline leaves; very rarely perennials without cauline leaves; fruiting pedicels much narrower than fruit (except some *Neotorularia*).
      4a. Fruits compressed; cotyledons accumbent.
        5a. Cauline leaves short petiolate, neither auriculate nor sagittate at base; trichomes simple and 2- or 3(or 4)-forked, never dendritic or stellate; fruit valves with a prominent midvein; seeds usually wingless . . . . . *Arabidopsis*

5b. Cauline leaves auriculate to sagittate at base, rarely petiolate; at least some of leaf trichomes dendritic or stellate; fruit valve without or with obscure midvein; seeds often winged . . . . . *Arabis*

4b. Fruits usually terete or 4-angled; cotyledons incumbent.

6a. Inflorescence axis flexuous; leaves divided into 3 or 5 filiform to narrowly linear segments . . . . . *Ianhedgea*

6b. Inflorescence rachis not flexuous; leaves various but never divided into filiform or narrowly linear segments.

7a. Flowers yellow.

8a. Cauline leaves petiolate; fruit apex strongly recurved or contorted; fruiting pedicels stout, nearly as thick as fruit . . . . . *Neotorularia*

8b. Cauline leaves auriculate, rarely sessile; fruit apex neither recurved nor contorted; fruiting pedicels slender, narrower than fruit . . . . *Olimarabidopsis*

7b. Flowers white, lavender, or purple, very rarely creamy white.

9a. Fruits glabrous.

10a. Cauline leaves petiolate; branched trichomes forked, rays always simple.

11a. Fruiting pedicels slender, narrower than fruit; seeds mucilaginous when wetted; fruits straight . . . . . *Arabidopsis*

11b. Fruiting pedicels stout, nearly as thick as fruit; seeds not mucilaginous when wetted; fruits often twisted . . . . . *Neotorularia*

10b. Cauline leaves sessile, often auriculate, sagittate, or amplexicaul, if short petiolate then plants canescent; at least some of the trichomes dendritic or stellate with some branched rays.

12a. All branched trichomes sessile; petals (6–)6.5–8(–9) mm; fruit short stipitate . . . . . *Pseudoarabidopsis*

12b. At least some of the branched trichomes distinctly stalked; petals 1.5–4(–5) mm; fruit sessile.

13a. Seeds biseriate; North America . . . . . *Halimolobos*

13b. Seeds uniseriate; Asia . . . . . *Crucihimalaya*

9b. Fruit pubescent.

14a. Inflorescence bracteate at least on lower half . . . . . *Crucihimalaya*

14b. Inflorescence ebracteate.

15a. Fruit with submalpighiaceous or short-stalked to subsessile stellate trichomes; septum lacking or perforated *Olimarabidopsis*

15b. Fruit with other trichome types; septum complete.

16a. Seeds not mucilaginous when wetted, uniseriate; fruit often strongly torulose and/or twisted; stems often decumbent; predominantly Old World . . . . . *Neotorularia*

16b. Seeds mucilaginous when wetted, mostly biseriate; fruit often smooth; stems not decumbent; exclusively New World . . . . . *Halimolobos*

Crucihimalaya Al-Shehbaz, O'Kane & Price, gen. nov. TYPE: *Crucihimalaya himalaica* (Edgeworth) Al-Shehbaz, O'Kane & Price.

Folia caulina sessilia vel subsessilia, auriculata vel raro nonauriculata; pili ramosi stipitati stellati saepe pilis simplicibus vel furcatis praesentibus; racemi bracteati vel ebracteati, valde elongati; sepala oblonga, nonsaccata; petala alba vel purpurea; fructus lineares, teretes, saepe glabri; stipitum nullum; septum completum; semina uniseriata vel raro biseriata, (15–)20–60(–75) per locula, oblonga, mucilaginosa; cotyledones incumbentes.

Herbs annual or biennial, rarely perennial with a caudex. Trichomes stalked, 1- or 2-forked, often mixed with simple and/or stellate ones, never dendritic. Stems erect to ascending, simple or branched basally and/or apically. Basal leaves rosulate or not, simple, entire or dentate, rarely lyrate or pinnately lobed. Cauline leaves sessile or subsessile, auriculate, sagittate, or rarely cuneate into a petiole-like base, entire, dentate, or rarely pinnately lobed, rarely absent and plants scapose. Inflorescences several- to many-flowered, corymbose racemes, elongated considerably in fruit; rachis straight; bracts present along entire inflorescence, or restricted to lowermost flowers, or absent. Sepals oblong, deciduous, erect, pubescent, base of inner pair not saccate. Petals white, lavender, or purple, spatulate. Stamens 6, slightly tetradynamous; anthers ovate or oblong, sagittate at base, obtuse at apex. Nectar glands confluent and subtending bases of all stamens. Ovules (30–)40–120(–150) per ovary. Fruit dehiscent, linear, terete or somewhat 4-angled to rarely compressed parallel to septum; valves with a distinct midvein, glabrous or rarely stellate hairy or puberulent, smooth or torulose; gynophore absent; septum complete; style to 1 mm long; stigma capitate, entire. Seeds uniseriate or rarely biseriate, (15–)20–60(–75) per locule, wing-

less, oblong, plump; seed coat minutely reticulate, mucilaginous when wetted; cotyledons incumbent.

Crucihimalaya, which means "cross Himalaya," is readily distinguished from *Arabidopsis* by having at least some stalked stellate trichomes (these sometimes mixed with simple or forked ones), sessile and auriculate to sagittate cauline leaves rarely subsessile into a petiole-like base, and bracteate or ebracteate inflorescences. *Arabidopsis* always has stalked forked trichomes, petiolate cauline leaves, and ebracteate inflorescences. Four species of *Crucihimalaya* (*C. axillaris*, *C. himalaica*, *C. lasiocarpa*, and *C. stricta*) have inflorescences bracteate at least on the lower half, and most of the remaining species often have the lowermost flower bracteate. However, this character can be very variable, and the presence of stellate trichomes and/or auriculate to sagittate cauline leaves should help in the separation of such species from *Arabidopsis*.

KEY TO THE SPECIES OF *CRUCIHIMALAYA*

1a. Fruit valves densely and coarsely stellate; pedicels pubescent all around; fruits often subappressed to rachis . . . . . 4. *C. lasiocarpa*
1b. Fruit valves glabrous or very rarely puberulent; pedicels glabrous adaxially, rarely (*C. wallichii*) pubescent all around; fruits not appressed to rachis.
2a. Cauline leaves distinctly auriculate or amplexicaul at base.
3a. Inflorescences bracteate at least along the lower portion; annuals or biennials . . . . . 6. *C. himalaica*
3b. Inflorescences ebracteate; perennials.
4a. Fruits divaricate; plants biennial; adaxial surface of lower cauline leaves predominantly with forked trichomes . . . . . 2. *C. orczinnikovii*
4b. Fruits erect; plants perennial; adaxial surface of lower cauline leaves predominantly with stalked stellate trichomes . . 1. *C. mollissima*
2b. Cauline leaves sessile or subsessile into a petiole-like base, neither auriculate nor amplexicaul, sometimes absent.
5a. Plants scapose; cauline leaves absent or only 1; Mongolia . . . . . 3. *C. mongolica*
5b. Plants with well-developed stems and several cauline leaves; Himalaya and southwest Asia.
6a. Lowermost flowers of main inflorescence bracteate; basal leaves entire to dentate, not canescent, withering by flowering or fruiting.
7a. Stem leaves adaxially with simple and forked trichomes, ovate to elliptic or oblong, rarely oblanceolate; plants 4–15(–20) cm tall; main inflorescence bracteate nearly throughout . . . . . 7. *C. axillaris*
7b. Stem leaves adaxially with stellate stalked trichomes, linear-lanceolate; plants (18–)30–85(–120) cm tall; only lowermost flowers of main inflorescence bracteate . . . . 5. *C. stricta*
6b. Lowermost flowers of main inflorescence ebracteate; basal leaves lyrate to pinnatifid, often canescent, persistent in flower and fruit.
8a. Petals (2–)2.5–3.5(–4.5) mm long; stem base and petioles of basal leaves often with simple trichomes (0.5–)0.8–1.5(–2) mm long; base of lower cauline leaves usually minutely auricled; plants from Nepal and Tibet west into Iran . . . . 8. *C. wallichii*
8b. Petals 4.5–5.5 mm long; stem base and petioles of basal leaves without simple trichomes; base of lower cauline leaves not auricled; plants of Sinai and western Saudi Arabia . . . . . 9. *C. kneuckeri*

1. Crucihimalaya mollissima (C. A. Meyer) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium mollissimum* C. A. Meyer, in Ledebour, Icon. Pl. Fl. Ross. Impr. Altai. Illust. 19. 1831. TYPE: [Russia], Altai, "Hab. in insulis atque ripis fl. Tschuja [Chuya River]," *C. A. Meyer s.n.* (holotype, LE; ?isotypes, P, W).

Distribution. Afghanistan, China, India, Kashmir, Kazakstan, Mongolia, Pakistan, Russia (Siberia), Tajikistan.

Reports of *Crucihimalaya mollissima* (as *Arabidopsis*) from Bhutan by Grierson (1984) and from the Chinese provinces Sichuan and Yunnan by An (1987) were based on misidentified plants of *C. himalaica*. An also reported the species from Gansu and Shaanxi, but we were unable to verify those records.

Schulz (1924) divided the species into eight varieties, of which var. *yunnanensis* O. E. Schulz is based on an immature plant of a species of *Arabis*, var. *afghana* O. E. Schulz is *Crucihimalaya wallichii*, and var. *griffithiana* (Boissier) O. E. Schulz is *Arabis bijuga* Watt. The remaining varieties were based on minor continuous differences in the indumentum and leaf margin and, therefore, do not merit recognition. None of Schulz's eight varieties were recognized in any subsequent taxonomic treatment.

2. Crucihimalaya ovczinnikovii (Botschantsev) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Arabidopsis ovczinnikovii* Botschantsev, in P. N. Ovczinnikov, Fl. Tadzhitskoi SSR 5: 625. 1978. TYPE: Tajikistan. Badachschan, fl. Gunt, canalis Chanif ca. urb. Chorog, 19 June 1966, *R. Kamelin s.n.* (holotype, LE; isotype, LE).

Distribution. Endemic to Tajikistan.

The species is most closely related to and sometimes difficult to separate from *Crucihimalaya mollissima*. The most reliable characters that separate the two species are listed in the key above.

3. Crucihimalaya mongolica (Botschantsev) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Arabis mongolica* Botschantsev, Bot. Zhurn. 60: 947. 1975. TYPE: Central Mongolia. Gobi of Altai Mt., Bain Tzagan, 4 Aug. 1931, *N. P. Ikonnikov-Galitzky & V. A. Ikonnikova-Galitzka 3805* (holotype, LE).

Distribution. Endemic to Mongolia.

Crucihimalaya mongolica is most closely related to *C. mollissima*; it is readily distinguished from this and the remaining species of the genus by the scapose inflorescences and the lack of or presence of a single non-auriculate cauline leaf. The species has incumbent cotyledons, and Botschantsev's (1975) original placement of the species in *Arabis* is erroneous because this genus always has accumbent cotyledons. Měsiček and Soják (1995) were correct in associating the species with *C. mollissima*.

4. Crucihimalaya lasiocarpa (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium lasiocarpum* J. D. Hooker & Thomson, J. Linn. Soc., Bot. 5: 162. 1861, not *S. lasiocarpum* F. Mueller, Fragm. 7: 20. 1869. *Sisymbrium bhutanicum* N. P. Balakrishnan, J. Bombay Nat. Hist. Soc. 67: 57. 1970. TYPE: Bhutan. *Griffith s.n.* (lectotype, designated by Jafri (1973), K; isolectotype, BM).

Microsisymbrium duthiei O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 9: 1089. 1927. Syn. nov. TYPE: India. Kumaon [Uttar Pradesh]: Dhauli Valley, 2300–2650 m, 7 Aug. 1886, *J. F. Duthie 5331* (holotype, DD; photo and fragments, B).

Sisymbrium monachorum W. W. Smith, Rec. Surv. Bot. India 6: 35. 1913. Syn. nov. TYPE: Tibet. Gompa Hill, Gayantse, 25 June 1907, *H. M. Stewart s.n.* (holotype, CAL;? isotype, E).

Arabidopsis lasiocarpa (J. D. Hooker & Thomson) O. E. Schulz var. *micrantha* W. T. Wang, Bull. Bot. Res., Harbin 8(3): 19. 1988. Syn. nov. TYPE: China. Yunnan: Deqin, 3000 m, July–Aug. 1935, *Wang Chi-wu 64727* (holotype, PE; isotype, PE).

Distribution. Bhutan, China, India, Nepal.

Balakrishnan (1970) proposed the name *Sisymbrium bhutanicum* to replace *S. lasiocarpum* J. D. Hooker & Thomson because he erroneously believed that *S. lasiocarpum* F. Mueller was the earlier homonym.

Schulz's (1927) original description of *Microsisymbrium duthiei* matches that of *C. lasiocarpa* in every morphological detail, and it appears that Schulz (1924) never examined any material of *C. lasiocarpa*, a species he placed in *Arabidopsis*. Schulz (1924, 1936) depended solely on the presence vs. absence of seed mucilage to separate *Microsisymbrium* from *Arabidopsis*, and it is likely that he did not observe seed mucilage in the material he described as *M. duthiei*.

5. Crucihimalaya stricta (Cambessèdes) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Malcolmia stricta* Cambessèdes, in Jacquemont, Voy. Ind. Bot. 4: 16. 1844. TYPE: NW Himalaya [India]. Simla (as Semla), *Jacquemont s.n.* (holotype, P; isotype, K).

Arabidopsis stricta (Cambessèdes) N. Busch var. *bracteata* O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 9: 1061. 1927. Syn. nov. TYPE: [India]. Kumaun, Deopata, Naini Tál, 2300 m, 4 July 1885, *J. F. Duthie 3835* (holotype, B).

Distribution. China, India, Kashmir, Nepal, Pakistan.

An's (1987) report of *Crucihimalaya stricta* (as *Arabidopsis stricta*) from Sichuan is based on misidentification of plants of *C. himalaica*. The reports in Schulz (1924), Jafri (1973), and Hajra et al. (1993) of the species from Afghanistan were based on collections (*Aitchinson 210* and *251*, BM and K) from Pakistan. A duplicate specimen at K of the Jacquemont collection from India (no locality was given, but it bears the numbers 2188 and "(786)") is definitely *C. himalaica* because it has large-auricled leaves and bracts. It is not part of the type collection of *C. stricta*, a species that never has auriculate leaves or bracts.

Crucihimalaya stricta was not reported from Nepal (Hara, 1979), though Schulz (1927) cited one collection (*Duthie 5352*) from Budhi village in western Nepal. We have examined another collection, *Stainton, Sykes & Williams 3365* (BM, E, G), that was collected from Jagat and misidentified as *Arabidopsis mollissima*.

6. Crucihimalaya himalaica (Edgeworth) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Arabis himalaica* Edgeworth, Trans. Linn. Soc. 20: 31. 1846. TYPE: [India]. "In glareosis Himala, alt. ped. 10,000–11,000, Mana," *Edgeworth s.n.* (holotype, K).

Arabis brevicaulis Jafri, Notes Roy. Bot. Gard. Edinburgh 22: 99. 1956. Syn. nov. TYPE: NW Himalaya. Karakorum, Zangia Harar, Hunza Valley, 3600 m, 5 July 1939, *R. S. Russell 1066* (holotype, BM).

Distribution. Afghanistan, Bhutan, China, India, Kashmir, Nepal, Pakistan, Sikkim.

Arabis brevicaulis was transferred by Jafri (1973) to *Arabidopsis*. He admitted that the species could conceivably be placed in *A. mollissima*. The specimens cited by Jafri under *A. mollissima* clearly represent a mixture of that species and *A. himalaica*. One of the specimens, *Bowes Lyon 849* (BM), was annotated by Jafri as the holotype of *Arabidopsis chitralica* Jafri, a name that was never published. The specimen was cited by Jafri (1973) as *A. mollissima*, and it is most likely the same as the type of *Arabis brevicaulis*.

On the basis of cited specimens, both *Arabidopsis himalaica* and *A. mollissima* were confused by Schulz (1924), Hedge (in Hedge & Rechinger, 1968), and Jafri (1973). The principal character used by these authors to separate these two species is the presence in *A. himalaica* of bracts along the entire length of the inflorescences and the lack in *A. mollissima* of bracts or their restriction to the lowermost few flowers of the inflorescence. However, this character shows tremendous variability in the same population or even on the same plant. In most plants of *A. himalaica* the uppermost portion of the inflorescence is ebracteate. For example, in *Lowndes 1166* (BM) one plant has the lowermost 24 flowers bracteate and another has only the lowermost 4 bracteate. In *Stewart 17986* (US) one plant has almost ebracteate inflorescences and another has fully bracteate inflorescences. Plants of *Crucihimalaya himalaica* are annual or biennial with coarse stellate and forked trichomes, at least basally bracteate inflorescences, slender fruits (0.4–)0.5–0.8(–1) mm wide, and seeds 0.5–0.8 mm long. By contrast, plants of *C. mollissima* are perennial with soft stellate trichomes, ebracteate inflorescences, fruits 1–1.5 mm wide, and seeds 0.8–1.1 mm long.

Plants from Chitral (Pakistan) treated by Jafri (1956, 1973) as *Arabis brevicaulis* and *Arabidopsis brevicaulis*, respectively, differ from typical *C. himalaica* in being perennials with only the basal one or two flowers bracteate, but they are perfectly at home in the species in trichome type, fruit width, and seed length. They might be recognized at the subspecific rank, but more material is needed for a sound conclusion to be reached.

7. Crucihimalaya axillaris (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium axillare* J. D. Hooker & Thomson, J. Linn. Soc., Bot. 5: 162. 1861. TYPE: Sikkim. Alt. 8,000–10,000 ft., *J. D. Hooker s.n.* (lectotype, designated by Jafri (1956), K; isolectotypes, B, G, W).

Microsisymbrium axillare (J. D. Hooker & Thomson) O. E. Schulz var. *brevipedicellatum* Jafri, Notes Roy. Bot. Gard. Edinburgh 22: 112. 1956. Syn. nov. TYPE: India. Lahul, Keylang, 3600 m, 8 June 1889, *G. Watt 2433* (holotype, E).

Microsisymbrium axillare var. *dasycarpum* O. E. Schulz, Pflanzenreich IV. 105(Heft 86): 160. 1924. Syn. nov. TYPE: Bhutan. *Griffith 1383* (holotype, CAL?; isotypes, K, P, W).

Microsisymbrium bracteosum Jafri, Notes Roy. Bot. Gard. Edinburgh 22: 112. 1956. Syn. nov. TYPE: India. Kuymaon, Bynas, ca. 2400 m, Apr. 1881, *J. R. Reid s.n.* (holotype, E).

Distribution. Bhutan, China, India, Kashmir, Nepal, Sikkim.

Schulz (1924) recognized plants with puberulent fruits as variety *dasycarpum*, but both glabrous and puberulent fruits can be found in the same population. Robust plants of this species were described by Jafri (1956) as *Microsisymbrium bracteosum*, while those with short pedicels and ebracteate uppermost flowers were described as *M. axillare* var. *brevipedicellatum*. However, these characters show continuous variation and, therefore, these two taxa do not merit recognition.

8. Crucihimalaya wallichii (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium wallichii* J. D. Hooker & Thomson, J. Linn. Soc., Bot. 5: 158. 1861. TYPE: [India]. Kumaon, *Wallich 4784* (lectotype, designated by Jafri (1973), K; isolectotype, BM).

Arabidopsis mollissima (C. A. Meyer) O. E. Schulz var. *afghanica* O. E. Schulz, Pflanzenreich IV. 105(Heft 86): 281. 1924. Syn. nov. TYPE: Afghanistan. *Griffith 1470* (holotype, K).

Arabidopsis russelliana Jafri, Notes Roy. Bot. Gard. Edinburgh 22: 97. 1956. Syn. nov. TYPE: Karakorum, Kero Lugma glacier, 3900 m, 27 July 1939, *R. S. Russell 1855* (holotype, BM).

Distribution. Afghanistan, Bhutan, China, India, Iran, Kashmir, Kazakstan, Kyrgyzstan, Nepal, Pakistan, Tajikistan, Turkmenistan, Uzbekistan.

Crucihimalaya wallichii is the most variable species in the genus, especially in the density of indumentum, division of basal and cauline leaves, length of fruiting pedicels, and length and degree of compression of fruit. The continuous variation in these characters has been adequately described by Hedge (in Hedge & Rechinger, 1968), and it is evident that no infraspecific taxa can be recognized. However, Jafri (1973) segregated two additional species, as *Arabidopsis taraxacifolia* (T. Anderson) Jafri and *A. russelliana* Jafri, based primarily on differences in the degrees of stem branching, style length, and petal size. In our opinion, these highly variable characters are unreliable and, therefore, these segregates do not merit recognition at any rank.

Crucihimalaya wallichii is closely related to *C. kneuckeri*, and the two species can be separated only by the characters in the key above.

Schulz (1927), in his original description of *Microsisymbrium flaccidum* O. E. Schulz, cited two syntypes, *Duthie 11055* and *Inayat 19172*, both of which are deposited at DD, with photos and fragments at B. The former collection was designated by Jafri (1973) as the lectotype, and there is an isolectotype at K. This is definitely an immature plant of a species of *Arabis*. The second collection, *Inayat 19172*, is a glabrescent form of *Crucihimalaya wallichii* with slightly lyrate leaves and incumbent cotyledons.

9. Crucihimalaya kneuckeri (Bornmüller) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium kneuckeri* Bornmüller, in A. Kneucker, Allgem. Bot. Zeitschr. 9: 45. 1904. TYPE: [Egypt]. Mt. Sinai, Dschebel Katharin, 5 Apr. 1902, *A. Kneucker s.n.* (holotype, JE; isotype, B).

Distribution. Saudi Arabia, Egypt (Sinai).

Schulz (1924) mixed the flower size of *Crucihimalaya kneuckeri* with that of *C. wallichii*. The latter has flowers as small as 2 mm long. More material of *C. kneuckeri* is needed to fully assess its overall variation.

Olimarabidopsis Al-Shehbaz, O'Kane & Price, gen. nov. TYPE: *Olimarabidopsis pumila* (Stephan) Al-Shehbaz, O'Kane & Price.

Folia caulina sessilia, minute vel valde auriculata; pili ramosi sessiles vel minute stipitati malpighiacei vel stellati, ramis simplicibus; racemi ebracteati, valde elongati; sepala oblonga, nonsaccata; petala flava; fructus lineares, teretes, saepe stellati vel malpighiacei; stipitum nullum; septum nullum vel perforatum vel completum; semina uniseriata, 9–30 per locula, oblonga, mucilaginosa; cotyledones incumbentes.

Herbs annual. Trichomes short-stalked or sessile, malpighiaceous and 3- or 4-rayed stellate. Stems erect to ascending, sometimes decumbent, simple or branched basally and/or apically. Basal leaves not rosulate, simple, entire or very rarely pinnately dissected. Cauline leaves sessile, minutely to conspicuously auriculate, entire to dentate. Inflorescences few- to several-flowered, ebracteate, corymbose racemes, elongated considerably or rarely slightly elongated in fruit; rachis straight. Sepals oblong, deciduous, erect, glabrous or pubescent, base of inner pair not saccate. Petals yellow or yellowish white, oblanceolate. Stamens 4 or 6 and only slightly tetradynamous; anthers oblong, rounded at base, obtuse at apex. Nectar glands confluent and subtending bases of all stamens. Ovules 18–60 per ovary. Fruit dehiscent, linear, terete; valves with a distinct midvein, pubescent with exclusively malpighiaceous and/or short-stalked stellate trichomes; gynophore absent; septum complete, perforated, or reduced to a rim; style obsolete or distinct and to 1 mm long; stigma capitate, entire. Seeds uniseriate, wingless, oblong, plump; seed coat minutely reticulate, slightly mucilaginous or not mucilaginous when wetted; cotyledons incumbent.

As delimited here, *Olimarabidopsis*, which means "formerly *Arabidopsis*," consists of three species all of which were previously placed in *Arabidopsis*. One of those species was described twice under two genera (as *Trichochiton umbrosum* Botschantsev & Vvedensky and 20 years later (see below) as *Arabidopsis eseptata* Hedge). The two questions most relevant to *Olimarabidopsis* are: First, is *Trichochiton* distinct from the closely related and earlier published *Cryptospora* Karelin & Kirilow? Second, is *T. umbrosum* correctly assigned to this genus? All species of *Cryptospora* have 2-lobed stigmas, large seeds 2.5–4.5 mm long, indehiscent fruits that break up at maturity into 1-seeded segments, some simple trichomes on the leaves and/or stems, white to lavender flowers, and non-auriculate cauline leaves (Botschantsev, 1963). The type species of *Trichochiton*, *T. inconspicuum* Komarov, has all of these characters. Therefore, we fully agree with Schulz (1936) and Rechinger (in Hedge & Rechinger, 1968) in reducing *Trichochiton* to synonymy of *Cryptospora* and in recognizing its type as *C. inconspicua* (Komarov) O. E. Schulz.

The answer to the second question is no. *Trichochiton umbrosum* has entire stigmas, small seeds to 1.3 mm long, readily dehiscent fruits, exclusively

stellate and malpighiaceous (never simple) trichomes, pale yellow flowers, and minutely auriculate cauline leaves. In our opinion, these differences are substantial, and *T. umbrosum* (= *Arabidopsis eseptata*) is herein assigned to a new genus, *Olimarabidopsis*, of three very closely related species.

Olimarabidopsis is readily distinguished from *Arabidopsis* by having yellow flowers, auriculate cauline leaves, and pubescent fruits. In contrast, *Arabidopsis* has white to lavender flowers, short petiolate stem leaves, and glabrous fruits. *Olimarabidopsis* is distinguished from small-flowered species of the closely related genus *Erysimum* by its auriculate cauline leaves and short-stalked branched trichomes. All species of *Erysimum* have petiolate cauline leaves and malpighiaceous and/or sessile 3–5-rayed stellate trichomes.

KEY TO THE SPECIES OF *OLIMARABIDOPSIS*

1a. Trichomes on fruit valve exclusively submalpighiaceous; seeds 1–1.3 mm long; fruit attenuate to apex; style obsolete; stamens 4 or rarely 6 . . . . . 3. *O. umbrosa*

1b. At least some of the fruit trichomes 3- or 4-rayed; seeds less than 1 mm long; fruit cuneate to apex; style distinct; stamens 6.

2a. Septum perforate; fruit 0.4–1(–1.5) cm long, 5–18(–20)-seeded . . . . . 2. *O. cabulica*

2b. Septum complete; fruit 1.5–3.2(–4) cm, (15–)22–40(–60)-seeded . . . . . 1. *O. pumila*

1. Olimarabidopsis pumila (Stephan) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium pumilum* Stephan, in Willdenow, Sp. Pl. ed. 4, 3(1): 507. 1800. TYPE: N Persia. [Kizlar], *Stephan s.n.* (holotype, LE; isotype, W).

Distribution. Afghanistan, Armenia, Azerbaijan, China, Georgia, India, Iran, Iraq, Israel, Jordan, Kazakstan, Kyrgyzstan, Lebanon, Oman, Pakistan, Russia, Syria, Tajikistan, Turkmenistan, Turkey, Uzbekistan.

Sisymbrium griffithianum Boissier was transferred to *Microsisymbrium* by Schulz (1924). An examination of the type and numerous other collections clearly shows that the species is a minor variant of *Olimarabidopsis pumila* with strongly reflexed instead of divaricate to ascending fruits. In fact, plants with reflexed and divaricate to ascending fruits are commonly found in the same population, as evidenced by *Botschantsev 111* (LE) from Uzbekistan, *Hedge & Wendelbo 2901* (E) from Afghanistan, and *Lammond 1026* (E, LE) from Pakistan. It is surprising, therefore, to have the same species cited by Schulz (1924) under two different genera, as *M. griffithianum* and *Arabidopsis pumila*. We agree with Hedge (in Hedge & Rechinger, 1968) in reducing *S. griffithianum* to synonymy of *Olimarabidopsis pumila* (as *A. pumila*).

2. Olimarabidopsis cabulica (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Sisymbrium cabulicum* J. D. Hooker & Thomson, J. Linn. Soc., Bot. 5: 161. 1861. TYPE: Afghanistan. *Griffith* [*1465*] (holotype, K).

Arabidopsis korshinskyi Botschantsev, Novit. Syst. Pl. Vasc. Acad. Sci. URSS 1965: 272. 1965. Syn. nov. TYPE: [Tajikistan]. Alaica Valley, near Katyn-Art, stony Kyzylsu, 13 July 1895, *S. Korshinsky 304* (holotype, LE).

Distribution. Afghanistan, W China, Kyrgyzstan, Tajikistan.

The type and other collections annotated by Botschantsev as *Arabidopsis korshinskyi* are indistinguishable from the type of *Sisymbrium cabulicum*. The latter was reduced by Jafri (1973) to synonymy of *Arabidopsis pumila*. However, the perforate septum, shorter fruits, and fewer seeds per locule (see the key above) readily distinguish plants of the two species herein placed in *Olimarabidopsis*. Furthermore, *O. cabulica* (reported as *A. korshinskyi*) is a hexaploid ($2n = 48$), whereas *O. pumila* is tetraploid ($2n = 32$) (Aryavand, 1983; Ginter & Ivanov, 1968; Polatschek, 1971).

An (1987) reported the species (as *Arabidopsis pumila* (Stephan) N. Busch var. *alpina* (Korshinsky) O. E. Schulz) from Xinjiang, but we have not seen any material from China.

3. Olimarabidopsis umbrosa (Botschantsev & Vvedensky) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Trichochiton umbrosum* Botschantsev & Vvedensky, Not. Syst. Herb. Inst. Bot. & Zool. Acad. Sci. Uzbekistan 12: 10. 1948. TYPE: [Tajikistan]. Samarkand region, shady places around Lake Koli-Kalan, 16 June 1916, *Lipsky s.n.* (holotype, TASH).

Distribution. Afghanistan, Tajikistan, Uzbekistan.

Arabidopsis eseptata Hedge was correctly reduced to synonymy of *Trichochiton umbrosum* by Pachomova (1974) and Junussov (1978), but Pachomova erroneously cited the authorship of the species by considering it as a new combination based on Komarov's (1896) *T. inconspicuum* var. *umbrosum* Komarov. Although they selected the same epithet for the species, Botschantsev and Vvedensky (1948) treated *T. umbrosum* as a new species and cited a holotype collected 22 years after Komarov's publication.

Pseudoarabidopsis Al-Shehbaz, O'Kane & Price, gen. nov. TYPE: *Pseudoarabidopsis toxophylla* (Bieberstein) Al-Shehbaz, O'Kane & Price.

Folia caulina sessilia, sagittato-amplexicaulia vel raro auriculata; pili ramosi sessiles stellati, ramis ramosis; racemi ebracteati, valde elongati; sepala oblonga, subsaccata; petala alba vel lavandula; fructus lineares, teretes, glabri; stipitum distinctum; septum completum; semina biseriata, 30–50 per locula, oblonga, mucilaginosa; cotyledones incumbentes.

Herbs biennial or perennial. Trichomes sessile, stellate, 4- or 5-rayed, with at least some rays branched. Stems erect to ascending, simple or branched basally. Basal leaves rosulate, often withered by fruiting time, simple, entire or dentate. Cauline leaves sessile, deeply sagittate-amplexicaul or rarely auriculate, entire to dentate. Inflorescences several-flowered, ebracteate, corymbose racemes, elongated considerably in fruit; rachis straight. Sepals oblong, deciduous, erect, glabrous or pubescent, base of inner slightly saccate. Petals white to lavender, spatulate. Stamens 6, prominently tetradynamous; anthers oblong, sagittate at base, obtuse at apex. Nectar glands confluent, subtending bases of all stamens, surrounding those of lateral ones. Ovules 60–100 per ovary. Fruit dehiscent, linear, terete; valves with obscure midvein, glabrous; gynophore distinct; septum complete; style distinct and to 1 mm long; stigma capitate, entire or slightly 2-lobed. Seeds biseriate, 30–50 per locule, wingless, oblong to ovoid, plump; seed coat minutely reticulate, slightly mucilaginous when wetted; cotyledons incumbent.

Pseudoarabidopsis is readily distinguished from *Arabidopsis* and *Erysimum* by having sessile, sagittate-amplexicaul cauline leaves, exclusively sessile, stellate trichomes with branched rays, and a distinct gynophore. In *Arabidopsis* the leaves are petiolate and never amplexicaul or sagittate, the trichomes are simple mixed with stalked forked ones, and the fruits are sessile or subsessile. In its stellate trichomes and sagittate-amplexicaul cauline leaves, *P. toxophylla* resembles *Capsella bursa-pastoris* (L.) Medikus. Although drastically different in fruit morphology, these two species show remarkable affinities on the basis of ITS results.

Pseudoarabidopsis toxophylla (Bieberstein) Al-Shehbaz, O'Kane & Price, comb. nov. Basionym: *Arabis toxophylla* Bieberstein, Fl. Taur.-Cauc. 3: 448. 1819. TYPE: Not designated. Busch (1939) selected the specimen collected from Perekop and housed at LE as the type. We have not seen this specimen.

Distribution. Afghanistan, western China, Kazakstan, Russia, Tajikistan.

Generic Placement of Species Previously Included in *Arabidopsis*

The following 59 binomials previously assigned to *Arabidopsis* are assigned to 14 genera, including *Arabidopsis*. Accepted taxa are in boldface, and synonyms, excluded, or doubtful taxa are in italics. Binomials marked with (*) are proposed in this paper.

Arabidopsis arenosa (L.) Lawalrée, Bull. Soc. Roy. Bot. Belg. 92: 242. 1960.

A. bactriana Ovczinnikov & Junussov, Fl. Tadzhitskoi SSR 5: 626. 1978. No material has been seen, but according to the original description, the species cannot be assigned to *Arabidopsis* because it is a pulvinate, scapose perennial with cylindric fruits, subbiseriate seeds, and leafless stems. It is likely that the plant belongs to *Crucihimalaya mongolica*.

A. brevicaulis (Jafri) Jafri, Fl. W. Pakistan 55: 272. 1973. = **Crucihimalaya himalaica** (Edgeworth) Al-Shehbaz, O'Kane & Price (*).

A. bursifolia (DC.) Botschantsev, Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 19: 106. 1959. The systematic position of this species is problematic and awaits further study. Berkutenko (1988) suggested that the North American (Greenland, Yukon, and Alaska) *Arabidopsis mollis* (Hooker) O. E. Schulz, which Rollins (1943, 1952, 1993) treated as *Halimolobos mollis* (Hooker) Rollins, is probably the same as Russian (Far East) *A. bursifolia* (DC.) Botschantsev and that *A. tschuktschorum* (Jurtzev) Jurtzev, which is known only from the type locality at Chegiton River (Chukutka), is probably an abnormal plant of *A. bursifolia*. Although *A. bursifolia* and *H. mollis* may well prove to be conspecific, we have not yet conducted extensive study on them, and our work on *Halimolobos* is still in progress. However, we are certain that none of these species belongs to *Arabidopsis*.

A. campestris O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 9: 1059. 1927. = **Crucihimalaya wallichii** (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price (*).

A. cebennensis (DC.) O'Kane & Al-Shehbaz, Novon 7: 325. 1997.

A. croatica (Schott) O'Kane & Al-Shehbaz, Novon 7: 325. 1997.

A. dentata (Allioni) Dalla Torre, Alpenfl. 115. 1899. = **Murbeckiella pinnatifida** (Lamarck) Rothmaler, Bot. Not. 1939: 469. 1939.

A. drassiana Naqshi & Javeid, J. Econ. Taxon. Bot. 7: 624. 1986. No material has been seen. The species is excluded from *Arabidopsis* because it has sessile amplexicaul leaves. Naqshi and Javeid (1986) provided an incomplete description and gave no mention of the type of trichomes, which are very important in the *Arabidopsis* complex, and whether the fruits are terete or flattened. Because they indicated that the linear fruits include only one or two seeds, it is possible that the plant is of hybrid origin.

A. erysimoides Hedge & Kit Tan, Pl. Syst. Evol. 156: 202. 1987. = **Erysimum hedgeanum** Al-Shehbaz, Novon 4: 1. 1994.

A. eseptata Hedge, Fl. Iran. 57: 334. 1968. = **Olimarabidopsis umbrosa** (Botschantsev & Vvedensky) Al-Shehbaz, O'Kane & Price (*).

A. gamosepala Hedge, Fl. Iran. 57: 334. 1968. = **Neotorularia gamosepala** (Hedge) Al-Shehbaz & O'Kane, Novon 7: 93. 1997.

A. glauca (Nuttall ex Torrey & A. Gray) Rydberg, Fl. Rocky Mt. 342. 1917. = **Thellungiella salsuginea** (Pallas) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 252. 1924.

A. griffithiana (Boissier) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Olimarabidopsis pumila** (Stephan) Al-Shehbaz, O'Kane & Price (*).

A. halleri (L.) O'Kane & Al-Shehbaz, Novon 7: 325. 1997.

A. himalaica (Edgeworth) O. E. Schulz, Pflanzenreich IV.105(Heft 86): 283. 1924. = **Crucihimalaya himalaica** (Edgeworth) Al-Shehbaz, O'Kane & Price (*).

A. huetii (Boissier) N. Busch, Acta Hort. Petrop. 28: 389. 1908. = **Murbeckiella huetii** (Boissier) Rothmaler, Bot. Not. 1939: 472. 1939.

A. kneuckeri (Bornmüller) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 277. 1924. = **Crucihimalaya kneuckeri** (Bornmüller) Al-Shehbaz, O'Kane & Price (*).

A. korshinskyi Botschantsev, Novit. Syst. Pl. Vasc. Acad. Sci. URSS 1965: 272. 1965. = **Olimarabidopsis cabulica** (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price (*).

A. lasiocarpa (J. D. Hooker & Thomson) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 282. 1924. = **Crucihimalaya lasiocarpa** (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price (*).

A. lyrata (L.) O'Kane & Al-Shehbaz, Novon 7: 325. 1997.

A. minutiflora (J. D. Hooker & Thomson) N. Busch, Fl Cauc. Crit. 3(4): 457. 1909 = **Ianhedgea minutiflora** (J. D. Hooker & Thomson) Al-Shehbaz & O'Kane, Edinb. J. Bot. (1999 in press).

A. mollis (Hooker) O. E. Schulz, Bot. Jahrb. Syst. 66: 97. 1933. = **Halimolobos mollis** (Hooker) Rollins, Rhodora 43: 480. 1941.

A. mollissima (C. A. Meyer) N. Busch, Fl. Sib. Or. Extr. 1: 136. 1913. = **Crucihimalaya mollissima** (C. A. Meyer) Al-Shehbaz, O'Kane & Price (*).

A. monachorum (W. W. Smith) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 282. 1924. = **Crucihimalaya lasiocarpa** (W. W. Smith) Al-Shehbaz, O'Kane & Price (*).

A. mongolica (Botschantsev) Měsiček & Soják, Folia Geobot. Phytotax. 30: 448. 1995. = **Crucihimalaya mongolica** (Botschantsev) Al-Shehbaz, O'Kane & Price (*).

A. multicaulis Pampanini, Sped. Ital. DeDilippi Himal., etc. 1913–1914, Ser. 2, 11 (Agg. Fl. Carac.): 160. 1934. = **Arabis tibetica** J. D. Hooker & Thomson, J. Linn. Soc., Bot. 5: 143. 1861.

A. neglecta (Schultes) O'Kane & Al-Shehbaz, Novon 7: 326. 1997.

A. novae-anglicae Britton, in Britton & Brown, Illus. Fl., ed. 2, 2: 176. 1913. = **Neotorularia humilis** (C. A. Meyer) Hedge & J. Léonard, Bull. Jard. Bot. Nat. Belg. 56: 394. 1986.

A. nuda (Bélanger) Bornmüller, Beih. Bot. Zentralbl. 33(2): 275. 1915. = **Drabopsis nuda** (Bélanger) Stapf, Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 51(2): 298. 1886.

A. ovczinnikovii Botschantsev, in P. N. Ovczinnikov, Fl. Tadzhitskoi SSR 5: 625. 1978. = **Crucihimalaya ovczinnikovii** (Botschantsev) Al-Shehbaz, O'Kane & Price (*).

A. parvula (Schrenk) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 269. 1924. = **Thellungiella parvula** (Schrenk) Al-Shehbaz & O'Kane, Novon 5: 309. 1995.

A. pedemontana (Boissier) O'Kane & Al-Shehbaz, Novon 7: 326. 1997.

A. pinnatifida (Lamarck) Ruprecht, Mém. Acad. Sci. St. Pétersb. Ser. 7, 15(2): 86. 1869. = **Murbeckiella pinnatifida** (Lamarck) Rothmaler, Bot. Not. 1939: 469. 1939.

A. pumila (Stephan) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Olimarabidopsis pumila** (Stephan) Al-Shehbaz, O'Kane & Price (*).

A. qiranica Z. X. An, Fl. Xinjiang. 2(2): 376. 1995. = **Sisymbriopsis mollipila** (Maximowicz) Botschantsev, Nov. Syst. Pl. Vasc. 3: 122. 1966.

A. richardsonii (Rydberg) Rydberg, Fl. Rocky Mt. 341. 1917. = **Neotorularia humilis** (C. A. Meyer) Hedge & J. Léonard, Bull. Jard. Bot. Nat. Belg. 56: 394. 1986.

A. russeliana Jafri, Notes Roy. Bot. Gard. Edinb. 22: 97. 1956. = **Crucihimalaya wallichii** (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price (*).

A. salsuginea (Pallas) N. Busch, Fl. Sib. 1: 136. 1913. = **Thellungiella salsuginea** (Pallas) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 252. 1924.

A. sarbalica Naqshi & Javeid, J. Econ. Taxon. Bot. 7: 621. 1985 (1986). No material has been seen. The species is excluded from *Arabidopsis* because the cauline leaves are minutely auriculate. The original description and illustration clearly support placing the species in *Crucihimalaya wallichii*. Naqshi and Javeid (1986) separated *A. sarbalica* from *A. wallichii* because the former has shorter fruits 2.5–3.2 mm long, but this fruit length falls within that of *C. wallichii*.

A. schimperi (Boissier) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Robeschia schimperi** (Boissier) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 360. 1924.

A. stenocarpa Rydberg, Torrea 7: 160. 1907. = **Halimolobos virgata** (Nuttall ex Torrey & A. Gray) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 290. 1924.

A. stewartiana Jafri, Notes Roy. Bot. Gard. Edinburgh 22: 96. 1956. We have not seen any material of this species. Jafri (1956) distinguished it from *Olimarabidopsis pumila* (as *A. pumila*) on the basis of having semi-amplexicaul instead of sagittate-amplexicaul leaves and glabrous instead of pubescent fruits. Leaf base is extremely variable in *O. pumila*, and glabrous fruits, which are very rare in the species, can be found in populations that have predominantly pubescent fruits. Because of the bright yellow flowers, the species does not belong to *Arabidopsis*. The detailed original description of *A. stewartiana* leaves no doubt that it is a minor variant of *O. pumila*.

A. stricta (Cambessèdes) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Crucihimalaya stricta** (Cambessèdes) Al-Shehbaz, O'Kane & Price (*).

A. suecica (Fries) Norrlin, Meddel. Soc. Fauna Fl. Fenn. 2: 12. 1878.

A. taraxacifolia (T. Anderson) Jafri, Fl. W. Pakistan, 55: 274. 1973. = **Crucihimalaya wallichii** (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price (*). For an excellent discussion on the variation in this species and synonymy, see Hedge (in Hedge & Rechinger, 1968).

A. tenuisiliqua (K. H. Rechinger & Köie) Jafri, Fl. W. Pakistan 55: 171. 1973. = **Arabis tenuisiliqua** K. H. Rechinger & Köie, Anz. Math.-Nat. Kl. Oesterr. Akad. Wiss. 7: 5. 1954. We have not seen the type or any material of this species, and we are following Hedge (in Hedge & Rechinger, 1968) in maintaining it in *Arabis*, though the species is anomalous in that genus because of its incumbent cotyledons. It is excluded from *Arabidopsis* because it has stellate fruit trichomes, and no species of this genus has stellate hairs or pubescent fruits. Therefore, Jafri's (1973) transfer of the species is unacceptable. It is likely that the species is related to *Crucihimalaya wallichii*, from which it differs by having larger flowers and smaller fruit.

A. thaliana (L.) Heynhold, in Holl & Heynhold, Clav. Gen. Fl. Sachsen 1: 538. 1842.

A. tibetica Naqshi & Javeid, J. Econ. Taxon. Bot. 7: 621. 1985 (1986). We have not seen the type of this species, but the name is illegitimate because it is a later homonym of the following species. The plant is excluded from *Arabidopsis* because it is a perennial with stellate trichomes. Naqshi and Javeid (1986) considered the species to be closely related to *Crucihimalaya himalaica* (as *A. himalaica*) and distinguished solely on the basis of having non-auriculate, distinctly veined cauline leaves. It remains to be seen whether or not the two are conspecific.

A. tibetica (J. D. Hooker & Thomson) Lan & C. H. An ex K. C. Kuan, Fl. Xizang. 2: 372. 1985. = **Arabis tibetica** J. D. Hooker & Thomson, J. Linn. Soc., Bot. 5: 143. 1861.

A. toxophylla (Bieberstein) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Pseudoarabidopsis toxophylla** (Bieberstein) Al-Shehbaz, O'Kane & Price (*).

A. trichocarpa R. F. Huang, in S. W. Liu, Fl. Qinghaica 1: 509. 1997. We have examined the holotype of this species, and on the basis of its pubescent fruits and bracteate lowermost portion of inflorescences, the species is excluded from *Arabidopsis*. The plant is a minor variant of *Neotorularia humilis* (C. A. Meyer) Hedge & Léonard.

A. trichopoda (Turczaninow) Botschantsev, Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 18: 104. 1957. Botschantsev (1959) was correct in his placement of this species in synonymy of *Arabidopsis bursifolia*. See discussion under this species.

A. tschuktschorum (Jurtsev) Jurtsev, Bot. Zhurn. 60: 240. 1975. See discussion under *Arabidopsis bursifolia*.

A. tuemurnica K. C. Kuan & C. H. An, Bull. Bot. Lab. North-East Forest. Inst. 1980(8): 44. 1980. = **Neotorularia humilis** (C. A. Meyer) Hedge & J. Léonard, Bull. Jard. Bot. Nat. Belg. 56: 394. 1986.

A. verna (Koch) N. Busch, Fl. Cauc. Crit. 3(4): 460. 1909. = **Drabopsis nuda** (Bélanger) Stapf, Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 51(2): 298. 1886.

A. virgata (Nuttall ex Torrey & A. Gray) Rydberg, Fl. Rocky Mt. 342. 1917. = **Halimolobos virgata** (Nuttall ex Torrey & A. Gray) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 290. 1924.

A. wallichii (J. D. Hooker & Thomson) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Crucihimalaya wallichii** (J. D. Hooker & Thomson) Al-Shehbaz, O'Kane & Price (*).

A. yadungensis K. C. Kuan & C. H. An, Fl. Xizang. 2: 375. 1985. An examination of the type collection reveals that the species is definitely a member of the *Arabis hirsuta* (L.) Scopoli complex. The immature fruits are strongly compressed and subappressed to rachis, and the cauline leaves are strongly auriculate, all of which are characters not found in any *Arabidopsis* species. The species is under study by the senior author in connection with the *Flora of China* project.

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